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Soluble polyphenols and carbohydrates in throughfall and leaf litter decomposition

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SUMMARY

Soluble polyphenols and soluble carbohydrates were measured in throughfall, litter leachate and litter remains of sugar maple (*Acer saccharum* Marsh) leaf litter in five different forest types in south-central Wisconsin, USA. Soluble polyphenols in throughfall ranged from 13 to 24 $kg.ha^{-1}.yr^{-1}$ and soluble carbohydrates from 35 to 59 $kg.ha^{-1}.yr^{-1}$ with the highest concentrations occurring during spring and autumn. Leaching accounted for less than half of total disappearance of solubles from the litter. Total decomposition rate and nitrogen dynamics were similar for litter in all five stands, but leaching of soluble carbohydrates differed among stands and was significantly related to amounts of soluble polyphenols in throughfall.

KEY-WORDS: Acer saccharum - *Carbohydrates - Decomposition - Leaching - Polyphenols - Throughfall.*

RÉSUMÉ

Des polyphénols et glucides solubles ont été mesurés dans la litière de feuilles d'érable (*Acer saccharum* Marsh) de cinq différents types de forêts du Wisconsin (USA) (écoulement direct, lessivats de litière, résidus de litière). Les polyphénols solubles liés à l'écoulement direct vont de 13 à 24 $kg/ha^{-1}/an^{-1}$ et les glucides solubles de 35 à 59 $kg/ha^{-1}/an^{-1}$, les concentrations les plus importantes ayant lieu au printemps et à l'automne. Moins de la moitié de la disparition totale des composants solubles de la litière est due au lessivage. Le taux de décomposition totale et la dynamique de l'azote sont les mêmes dans la litière des 5 sites, mais le lessivage des glucides solubles diffère selon les sites et est lié de façon significative aux quantités de polyphénols solubles apportés par l'écoulement direct.

MOTS-CLÉS : Acer saccharum - *Glucides - Décomposition - Lessivage - Polyphénols - Écoulement direct.*

1. — INTRODUCTION

Soluble compounds comprise a large fraction of the initial dry matter of deciduous leaf litter (COLDWELL & DELONG, 1950; DAUBENMIRE & PRUSSO, 1963). Some of these soluble compounds may be readily leached from the litter or used by litter inhabiting microorganisms during early stages of decomposition (WILLIAMS & GRAY, 1974; SWIET *et al.*, 1979). The rapid disappearance of these materials will result in high rates of mass loss from litter which has initially high concentrations of soluble compounds.

Two compounds which may be important in affecting decomposition rate are carbohydrates and polyphenols, particularly tannins. HEAL *et al.* (1978) observed

that mass loss from a variety of litter types was positively correlated with initial soluble carbohydrate concentrations and negatively correlated with initial tannins plus lignin. Soluble carbohydrates are readily metabolized by many microorganisms and should disappear rapidly from litter (*cf.* NYKVIST, 1963). However, their presence may inhibit the production of some polysaccharide degrading enzymes by product or catabolite repression (WHITTAKER, 1971) and delay the onset of cellulose and hemicellulose degradation. Soluble polyphenols may also be leached or metabolized by litter inhabiting organisms, but they may have a negative effect on decomposition by inhibiting microorganisms (HARRISON, 1971; THEANDER, 1978), by tanning proteins and reducing nitrogen availability (HANDLEY, 1961) or inactivating enzymes (FEENEY, 1976). These two classes of compounds are present in litter and in throughfall falling onto the litter. Microorganisms degrading litter could therefore be affected by soluble compounds from both sources.

Because soluble carbohydrates and polyphenols may be important in the initial stages of litter decomposition, their movements in throughfall and litter are of interest. This study was conducted with the following objectives: 1) determine the amounts of soluble carbohydrates and polyphenols in throughfall in five forest types occurring in south-central Wisconsin, USA; 2) determine the extent of leaching of soluble carbohydrates and polyphenols from sugar maple (*Acer saccharum* Marsh) leaf litter during the period when loss of solubles is an important component of total litter mass loss; 3) determine the effects of soluble organics in throughfall on sugar maple leaf litter decomposition.

2. — SITE DESCRIPTION

The study was conducted on Blackhawk Island in the Wisconsin River, south-central Wisconsin, USA (43° 38′ N, 89° 47′ W) at an altitude of 270-280 m. The 30-year mean annual temperature was + 7.6° C and the mean annual precipitation was 800 mm based on records at the Wisconsin Dells weather station 2 km south of the Island. Soil temperatures at 10 cm in all stands were at or near 0° C during January through March in both 1980 and 1981 and reached a maximum of 17-18° C in late July and early August 1981.

Five distinct forest stands, which can be characterized by their dominant vegetation and soil type, were selected on the 70 ha island: 1) sugar maple—Alfisol, 2) white pine (*Pinus strobus* L.)—Spodosol, 3) white oak (*Quercus alba* L.)—Alfisol, 4) hemlock (*Tsuga canadensis* (L.) Carr.)—Histosol and 5) aspen (*Populus grandidentata* Michx.)—plowed Alfisol. With the exception of the aspen stand, which had succeeded onto a previously plowed field, the stands were edaphic climax forests with

TABLE I. — *Selected soil characteristics in the five study stands.*

Stand	Soil type	Silt+clay (%)	Humus type
Sugar maple	Typic Hapludalf	69	Mull
Hemlock	Folist	Organic	Mor
White oak	Typic Hapludalf	65	Mor
Aspen	Plowed Alfisol	59	Mull
White pine	Entic Haplorthod	17	Mor

no evidence of past disturbance. Dominant trees in the climax stands were 100-200 years old. Trees in the aspen stand were approximately 50 years old. Selected soil characteristics are presented in table I. The vegetation, soils and geology of Blackhawk Island, and of these stands in particular, have been described by Pastor *et al.* (1982). Because of their proximity to one another, all stands had nearly identical precipitation and temperature regimes.

3. — MATERIALS AND METHODS

3.1. *Field methods*

Sugar maple leaf litter was collected within two days of its abscission during late October 1980 from fiberglass screens spread on the forest floor of the sugar maple stand. No precipitation occurred during the collection period. Litter was dried at room temperature (20-25° C) for several days. Samples weighing approximately 4.5 g were placed into 15 × 15 cm polyester litter bags which had a mesh size of 0.1 mm. Subsamples were retained for the determination of initial moisture and chemical content.

Throughfall was collected in the five stands using plastic funnels, 162 mm diameter, attached through rubber stoppers to 4-lit plastic reservoirs. Screen was placed in the funnel necks to prevent large particulates from entering the collectors. Phenyl mercuric acetate dissolved in dioxane-water was added to the collectors initially and after every collection to prevent microbial growth. Tops of collectors were 30 cm above the forest floor. Precipitation was collected at the Wisconsin Dells weather station near Blackhawk Island using two identical collectors.

Nine pairs of collectors were located randomly in each stand and a litter bag containing about 4.5 g of sugar maple leaf litter was placed in one funnel of each pair. Litter bags were also located randomly on the forest floors of each stand within 15 m of the throughfall collectors. The amount of litter per funnel area (206 cm^2) was equivalent to 2.2 Mg/ha. The amount per litter bag area (225 cm^2) was equivalent to 2.0 Mg/ha. Both values corresponded closely to measured annual leaf litter fall in all but the hemlock stand, which had a lower leaf litter fall (McClaugherty, unpublished). Litter bags and collectors were installed 20 November 1980, immediately after most deciduous leaf litter had fallen.

Throughfall was collected after about 2 lit, or the equivalent of 10 cm of precipitation, had accumulated. Five litter bags were collected from the funnels in each stand in November 1981. Four litter bags were removed from the forest floor of each stand at eight collection dates during the year. Throughfall, litter leachate and litter bag collections were continued up to 550 days when it had become apparent that no further decreases in the percent of initial soluble materials remaining were likely to occur.

3.2. *Laboratory methods*

Throughfall and precipitation samples were returned to the laboratory, stored at 3° C and analyzed within 48 h. Soluble carbohydrates were determined using a phenol-sulfuric acid method (Dubois *et al.*, 1956) with glucose as the standard. Soluble polyphenols were analyzed using the Folin-Denis method (Allen *et al.*, 1974) with tannic acid as the standard.

Collected litter bags were returned to the laboratory, immediately dried at 60° C to constant mass and weighed. Samples were ground to pass a 1 mm mesh screen and were extracted successively with dichloromethane (Tappi, 1976) and hot (100° C) water (Tappi, 1975). Hot-water extracts were analyzed for soluble carbohydrates and polyphenols as described above. Ground litter samples were analyzed for moisture (105° C for 48 h) and ash (450° C for 8 h). Total organic nitrogen was determined on samples before and after extraction using a sulfuric acid-hydrogen peroxide digestion (Miller & Miller, 1948) followed by a colorimetric analysis for ammonium using a Technicon Autoanalyzer (Technicon Industrial Systems, 1977). Soluble nitrogen was estimated by the difference in nitrogen content before and after extraction. Results are given on an ash-free dry matter basis.

3.3. *Statistical methods*

Analysis of variance was used to detect significant differences among means of treatments (funnel *vs.* forest floor) and stands for each group of compounds. When significant differences were found, differences between pairs of means were tested using the Studentized Range (SNEDECOR & COCHRAN, 1967, p. 272). A significance level of $p < 0.05$ was used throughout.

4. — RESULTS

4.1. *Precipitation*

Soluble carbohydrates and polyphenols were detected in precipitation at trace levels. Mean amounts detected were rarely significantly greater than zero. Thus, soluble organics found in throughfall were derived almost entirely from the forest canopy.

4.2. *Throughfall*

Soluble carbohydrates and polyphenols were present in throughfall at all times except during winter (December through March). Cumulative amounts for each year are shown in figure 1. Soluble polyphenols were most abundant in throughfall immediately after budbreak during the period of rapid leaf expansion. Soluble polyphenols were also abundant in throughfall during abscission and leaf fall. Soluble carbohydrates were most abundant in throughfall during budbreak. The higher concentrations of solubles during spring may be due to a greater leaching potential for rapidly expanding foliage than for mature foliage. The large amounts of leaching from the canopy observed in autumn may relate to disruption of cells during senescence and possibly frost.

Amounts of both soluble carbohydrates and polyphenols in throughfall were significantly different between some stands. Sugar maple and white oak forest floors received the most polyphenols, more than 23 $kg.ha^{-1}.yr^{-1}$. The other three stands received smaller amounts and were not significantly different from one another. Amounts of soluble carbohydrates in throughfall were even larger, between 35 and 59 $kg.ha^{-1}.yr^{-1}$. The amount of soluble carbohydrates in throughfall in a particular stand was not proportional to the amount of soluble polyphenols in throughfall in that stand.

There were no significant differences among stands in throughfall volumes. Although deciduous canopies would be expected to retain less precipitation than conifers during winter, more than 85 % of the annual precipitation fell when the deciduous canopies were expanded.

4.3. *Litter leachate*

During the first year of incubation, throughfall percolating through litter was further enriched with soluble carbohydrates and soluble polyphenols from the decomposing leaf litter. The difference between amounts of solubles in litter leachate and in throughfall can be considered as net leaching. It is important to recognize that this is net leaching, because some solubles in throughfall may be retained on the litter and metabolized by microorganisms or transformed into insoluble forms, resulting in an underestimate of gross leaching.

Cumulative net leaching of soluble carbohydrates and polyphenols expressed as a percent of the initial amount of each constituent is illustrated in figure 2. The net

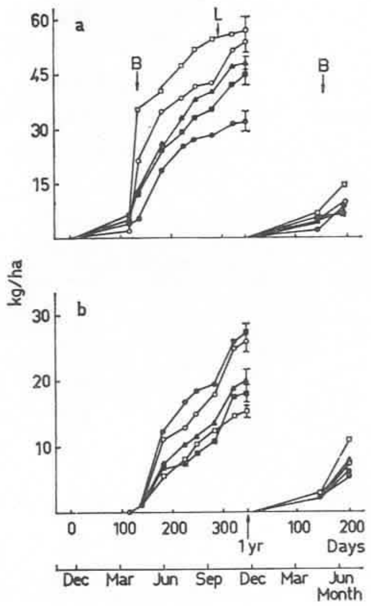

FIG. 1.

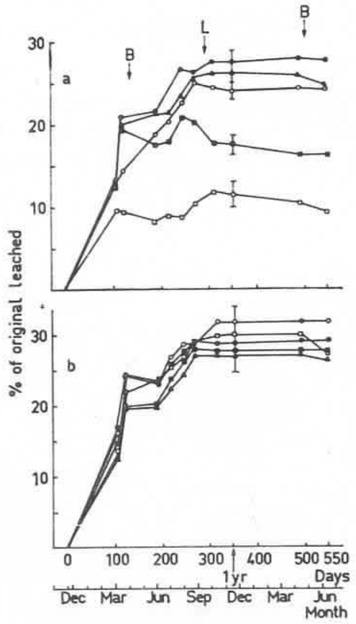

FIG. 2.

FIG. 1. — Cumulative amounts (kg/ha) each year of soluble carbohydrates (*a*) and soluble polyphenols (*b*) in throughfall through time (days) in five Wisconsin forests: ○: sugar maple, □: hemlock, ●: white oak, ■: aspen, ▲: white pine. Collections began 20 November 1980. Time of bud break and leaf fall are indicated by *B* and *L* respectively. Standard errors are shown at the one year sampling and are representative. $N = 9$ for each collection in each stand.

FIG. 2. — Cumulative net leaching of soluble carbohydrates (*a*) and soluble polyphenols (*b*) from sugar maple leaf litter through time (days) in leaching funnels in five Wisconsin forests: ○: sugar maple, □: hemlock, ●: white oak, ■: aspen, ▲: white pine. Net leaching is expressed as a percent of the original amount of soluble substances present in the litter. Net leaching was calculated as the difference between amounts of solubles in litter leachate and in throughfall. Collection began 20 November 1980. Standard errors are shown only for the one year sampling, but are representative. $N = 9$ for each collection in each stand.

amount of leached materials increased rapidly for both groups of compounds during the first few months of decomposition, but no additional leaching was measured after the first year. In some cases, the amount of solubles in throughfall was greater than in leachate, resulting in a negative net leaching and a decline in cumulative net leaching. Net leaching of soluble carbohydrates was negative after the first year in the aspen and hemlock stands, indicating that microorganisms on the litter in those two stands were utilising some of the soluble carbohydrates received from throughfall. Since there were no significant differences between amounts of soluble carbohydrates remaining in funnel-incubated leaf litter across all five stands (see table II) we can assume that leaching differences for soluble carbohydrates were due largely to differences in microbial metabolism. In contrast to soluble carbohydrates, soluble polyphenols followed nearly identical leaching patterns in all stands.

4.4. *Solubles remaining in litter*

Amounts of soluble organics remaining in sugar maple leaf litter decreased much more rapidly than could be accounted for by leaching. Percentages of original dry

TABLE II. — *Amount of soluble compounds and organic nitrogen initially and after one year in sugar maple leaf litter. Litter was incubated in litter bags on the forest floor* (FF) *or in leaching funnels* (FUN) *in five forest stands: sugar maple* (SM), *hemlock* (HEM), *white oak* (WO), *aspen* (ASP) *and white pine* (WP). *Means may be compared using Studentized range* (SR) *with 95 % confidence.*

	Initial mg/g	After one year mg/g initial dry matter										
		SM		*HEM*		*WO*		*ASP*		*WP*		*SR*
		FF	*FUN*	*FF*	*FUN*	*FF*	*FUN*	*FF*	*FUN*	*FF*	*FUN*	(95 %)
Hot-water solubles	336	59	47	56	42	61	59	31	42	55	47	4.7
Soluble carbohydrates	72	13	10	18	13	16	11	7.9	9.2	13	10	3.9
Soluble polyphenols	97	8.3	3.6	10.5	3.8	10.0	5.5	3.1	3.8	8.2	4.4	1.8
Organic nitrogen	8.3	7.7	6.1	6.5	6.3	6.5	6.7	7.2	6.3	7.1	6.6	1.2
Dry matter	1,000	416	399	456	419	417	426	393	417	409	402	72

matter, hot water solubles, soluble carbohydrates and soluble polyphenols remaining in sugar maple leaf litter incubated in forest floor litter bags in the sugar maple stand are shown in figure 3. After 50 days, the litter contained only about half of its initial content of soluble polyphenols and by early summer, 214 days after installation, only about 15 % of the original amount remained. Soluble carbohydrates disappeared more slowly than either total hot water solubles or soluble polyphenols, but losses were similar after one year.

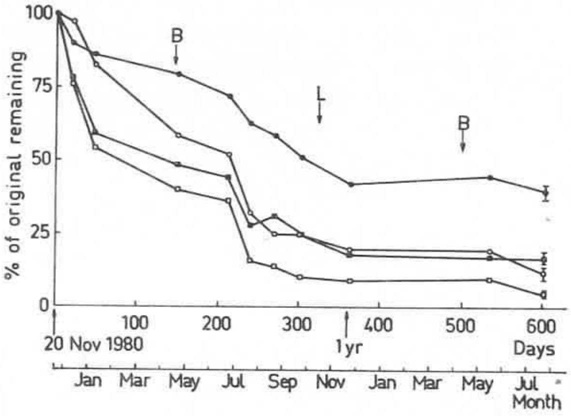

FIG. 3. — Percent of original dry matter (●), hot-water solubles (■), soluble carbohydrates (o) and soluble polyphenols (□) remaining in sugar maple leaf litter incubated in litter bags on the forest floor of a Wisconsin sugar maple forest. Incubations began on 20 November 1980. Standard deviations are shown for the final collection. $N = 4$ for each collection date and material.

Dry matter and all groups of soluble compounds exhibited a period of relatively slow disappearance during the winter of 1980-1981 when the soil temperature was at or near 0° C and a relatively more rapid disappearance during July 1981 when soil temperatures were at their maximum (fit. 3). These patterns suggest that decay rates reflect seasonal or temperature dependent biological activity.

Amounts of solubles leached from litter and the amounts remaining in litter can be compared with amounts initially present. The difference is an estimate of respiration

plus microbial or chemical conversion to insoluble or undetectable materials. Results of this calculation are shown in table III. Approximately two-thirds of the soluble compounds initially present were unaccounted for after one year, having been respired or converted into insoluble materials. This portion, calculated by difference, also includes the measurement error.

TABLE III. — *Percentages of soluble carbohydrates and soluble polyphenols in sugar maple leaf litter which were leached* (L), *remaining* (R) *or converted* (C) *during the first year of incubation in different stands. The percentage converted was calculated by difference.* N = *9 for percent leached;* N = *4 for percents remaining and converted. Studentized range provided for comparing means with 95 % confidence.*

Stand	Soluble carbohydrates			Soluble polyphenols		
	L	*R*	*C*	*L*	*R*	*C*
Sugar maple	23.9	13.3	62.8	31.6	3.7	64.7
Hemlock	11.3	18.0	70.0	29.9	3.9	66.2
White oak	27.2	15.4	57.4	28.5	5.7	65.8
Aspen	17.2	12.7	70.1	27.5	3.9	68.6
White pine	26.1	13.4	60.5	26.8	4.6	68.6
Studentized range ..	4.14	4.11	6.77	3.84	2.89	3.74

Although there were some significant differences between amounts of solubles remaining in litter incubated in funnels and on the forest floor, these differences were small relative to the amounts initially present in the litter. Since the total mass losses in all stands and treatments were not significantly different (table II) it is probable that the behaviour of solubles was similar in the two treatments.

5. — DISCUSSION

5.1. *Microorganisms and soluble substances*

Leaching as defined in this study is the movement of soluble compounds out of the litter-microorganism complex. Once in the forest floor, leached soluble compounds may be utilized by microorganisms or transformed into insoluble compounds. Thus, most soluble materials may not move far from the litter-microorganism complex before undergoing transformations (*cf.* NYKVIST, 1963). In the hemlock and aspen stands, where lesser amounts of carbohydrates were leached from litter, the microorganisms in the litter-microorganism complex probably utilized the solubles before they were leached. That these stands had microorganisms which were more efficient at retaining soluble carbohydrates is also indicated by the negative net leaching observed after the first year, which was described above.

Soluble polyphenols may be inhibiting microbial utilization of carbohydrates. The amount of carbohydrates leached after one year was significantly correlated with the amount of polyphenols in throughfall ($r = 0.884$, $p < 0.05$). This indicates that increased amounts of polyphenols in throughfall inhibited microbial utilization of soluble carbohydrates and allowed increased leaching. Differences in leaching of soluble carbohydrates did not appear initially (see fig. 2 *a*), but only after much of the initial soluble polyphenols had disappeared from the litter (see fig. 3).

5.2. *Soluble carbohydrates*

Soluble carbohydrates were less abundant in litter and more abundant in throughfall than were soluble polyphenols. Sugar maple leaf litter initially contained an average of 317 mg of soluble carbohydrates per funnel or the equivalent of 151 kg/ha. After one year internal amounts of soluble carbohydrates had declined to a mean of 48 mg per funnel or 23 kg/ha. Soluble carbohydrates in throughfall ranged from 63 $mg.funnel^{-1}.yr^{-1}$ in the white oak stand to 127 $mg.funnel^{-1}.yr^{-1}$ in the hemlock stand, or the equivalent of 35 to 59 $kg.ha^{-1}.yr^{-1}$, respectively. Thus the amounts of soluble carbohydrates in throughfall during the first year were between 23.1 and 39.3 % of the amounts in fresh litter.

Some of the soluble carbohydrates in throughfall may have come from insect excreta, particularly from aphids (Aphididae). Contributions from this source would be greatest during the middle of the growing season when insect population size and activity were at a maximum (LLEWELLYN, 1972). Since amounts of soluble carbohydrates in throughfall were greatest during spring and early summer (fig. 2) it is unlikely that insect excreta accounted for a large portion of the soluble carbohydrates in throughfall.

Some of the soluble carbohydrates in litter leachate may have been derived from the depolymerization of polysaccharides. Any leaching of materials derived from depolymerization would result in an overestimate of the leaching of soluble substances. The amount of leached soluble carbohydrates derived from polysaccharides was probably low for at least two reasons. First, microbial production of depolymerizing enzymes is likely to be low during periods when soluble carbohydrates are abundant due to product or catabolite repression (WHITTAKER, 1971). Second, depolymerizing enzymes are produced by microorganisms which are presumably capable of utilizing the soluble products of their enzymes. Thus it seems likely that most soluble carbohydrates derived from polysaccharides would be utilized by the microorganisms which produced the depolymerizing enzymes rather than being leached.

5.3. *Soluble polyphenols*

Initial amounts of soluble polyphenols in sugar maple leaf litter and amounts lost by leaching and conversion during the first year were quite large relative to amounts in throughfall. Initially, sugar maple leaf litter contained an average of 427 mg of soluble polyphenols per funnel or the equivalent of 204 kg/ha. After one year, internal amounts of polyphenols in funnel-incubated litter had dropped to a mean of 16 mg per funnel or 7.5 kg/ha, lower than the amounts remaining in litter incubated on the forest floor (see table II). Polyphenols in throughfall ranged from 13 $kg.ha^{-1}.yr^{-1}$ in the hemlock stand to 24 $kg.ha^{-1}.yr^{-1}$ in the white oak stand, or between 6.3 and 11.6 % of amounts initially present in sugar maple leaf litter, much lower than for soluble carbohydrates.

Even though the amounts of soluble polyphenols within litter were large relative to amounts in throughfall, the tanning potential of internal polyphenols may have differed from that in throughfall polyphenols, and the types of polyphenols in throughfall may have varied between stands and during the course of the year. The qualitative properties of the polyphenols in throughfall may have been different in spring and autumn. FEENEY & BOSTOCK (1968) found condensed tannins to be more abundant in red oak leaves during May, but hydrolysable tannins increased from 0.5 % in April to 5 % in September.

Qualitative differences between soluble polyphenols may affect their biological activity (ZUCKER, 1983). For example, TRÉMOLIÈRES & CARBIENER (1981) found that differences between oxygen absorption in extracts of litter depended on both the amount and nature of the polyphenols present. DAVIES *et al.* (1964) noted that the degree of polymerization of condensed tannins in leaves increased during senescence and after leaf fall. Furthermore, ROUX (1972) found that the tanning properties of condensed tannins did not increase appreciably after the molecule had polymerized above the 10-unit size. Thus there may not be a simple correlation between the amount of soluble polyphenols present in leaf litter or throughfall and their biochemical activity.

Amounts of soluble polyphenols leached and remaining were consistent across all stands, unlike the soluble carbohydrates (table III). Leaching of polyphenols was not suppressed in the hemlock and aspen stands. If the lower leaching of soluble carbohydrates in those two stands was due to greater microbial metabolism, it is interesting that these differences were not reflected in soluble polyphenol leaching. If the microorganisms which process soluble polyphenols are different than those that process carbohydrates, it is probable that soluble polyphenols in throughfall would affect the two groups differently. It is also possible that some of the unaccounted for soluble polyphenols were precipitated with proteins or other organic (HANDLEY, 1961; HAIDER *et al.*, 1965) rather than being metabolized by microorganisms. In addition, some of the throughfall polyphenols were probably rapidly condensed, forming insoluble or recalcitrant substances similar to humic substances (MANGENOT *et al.*, 1966). Thus if the soluble polyphenols in throughfall in different stands possessed qualitative differences which resulted in different degrees of condensation, then their effect on microorganisms and litter decomposition could also differ.

5.4. *Hot-water soluble substances*

Total hot-water soluble contents of the litter disappeared rapidly and accounted for nearly half the mass lost from sugar maple leaves during the first year (table II and fig. 3). Between 82 and 91 % of the initial hot-water solubles were lost during the first year accounting for 28 to 31 % of the initial dry matter. Significant differences in total hot-water soluble contents remaining after one year occurred among stands and between treatments (funnels *vs.* forest floor) within stands. As for soluble carbohydrates, these differences were quite small relative to the total mass loss of hot-water solubles. Because hot-water solubles account for a large portion of the mass lost during the initial stages of sugar maple leaf litter decomposition, a close relationship should exist between initial hot-water soluble concentrations and initial rates of mass loss for other species of leaf litter. This hypothesis is currently being tested on Blackhawk Island for six species of leaf litter.

5.5. *Soluble polyphenol-nitrogen interactions*

Soluble polyphenols may form complexes with proteins and reduce the mobility of nitrogen in an ecosystem (HANDLEY, 1961; HAIDER *et al.*, 1965). If this process is occurring in the sugar maple leaf litter, the amount of nitrogen remaining would be expected to be highest in materials receiving the greatest amounts of soluble polyphenols in throughfall. In this study there were no differences in nitrogen retention in leaf litter after one year even though there was a nearly two-fold range in the amount of soluble polyphenols in throughfall across the stands. This may be due to the fact that internal concentrations of soluble polyphenols in the leaf litter were quite

high, as described above, and additional polyphenols in throughfall had little effect.

Most of the soluble nitrogen in the litter was transformed into insoluble forms almost immediately after litter fall, probably by incorporation into polycondensates formed by the action of foliar or fungal phenoloxidases (MANGENOT *et al.*, 1966). Sixty-six percent of the total nitrogen initially present in sugar maple leaf litter was soluble in hot water. After three weeks, only 25 % of the total nitrogen was soluble in hot water. Although 7 % of the initial nitrogen was lost from the litter during this time, the amount did not account for the large decrease in hot-water soluble nitrogen, rather the decrease in soluble nitrogen was balanced largely by an increase in insoluble nitrogen. Apparently, substances present in fresh litter were more important in making nitrogen insoluble than were soluble polyphenols in throughfall.

CONCLUSION

Large amounts of soluble carbohydrates and polyphenols entered the forest floors in all five stands studied. The majority of these substances were deposited in spring and autumn during budbreak and leaf expansion and again at leaf abscission. Although significant differences were found among stands in throughfall concentrations of soluble carbohydrates and polyphenols, these differences had no detectable effect on total decomposition rate or nitrogen retention in sugar maple leaf litter, but soluble polyphenols appeared to have some effect on the processing of soluble carbohydrates. The probable importance of differences in the quality of soluble polyphenols, as opposed to the quantity, was discussed.

Losses of total hot-water soluble matter from sugar maple leaf litter during the first year of decay were large and accounted for nearly half of the total mass lost. Leaching of soluble polyphenols was similar in all stands, but leaching of soluble carbohydrates differed among stands. It was suggested that these differences were due to differences in microbial metabolism.

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